A PHYLOGENETIC STUDY OF THE TERMINAL ABDOMINAL SEGMENTS AND APPENDAGES IN SOME FEMALE APTERYGOTAN AND LOWER PTERYGOTAN INSECTS.[1]

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In a previous paper (Crampton, 1917*b*) the insects here discussed were grouped into three superorders whose principal diagnostic characters were there given. Strange to say, the neck and thoracic structures furnish far more definite characters for grouping these insects than the terminal abdominal structures of the female do; so that the following brief discussion is intended mainly to serve as the basis for a subsequent more detailed comparison of these parts in the lower orders, and also as the basis of a further study of the modifications met with in the higher insects, from the standpoint of phylogeny. For the material from which the accompanying rough sketches were made, I am indebted to the kindness of Dr. S. C. Ball, Mr. A. N. Caudell, Prof. R. A. Cooley, Mr. C. C. Gowdey, Dr. A. D. Imms, Mr. J. A. Rehn, and Dr. E. M. Walker.

Handlirsch (Die Fossilen Insekten) does not include the Apterygotan insects in the same class with the Pterygotan forms, but, when one makes a careful comparison of the various anatomical structures in the two groups, the fundamental resemblances point to a very close relationship between the Apterygota and lower Pterygota. Indeed, the differences between the lower Pterygota and the higher Pterygota (aside from the presence of wings) is infinitely greater than between the Lepismoid representatives of the Apterygota, and the lower Pterygotan insects. The striking similarity between the head of a Lepismid and that of a nymphal Plecopteron has already been pointed out,[2] and the similarity between the terminal abdominal segments of a Lepismid and those of a lower Pterygotan insect is no less fundamental. Thus the suranal plate labeled "11" in fig. 8, of a lower

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[2] Ent. News, for November, p. 398.

Pterygotan insect, is represented by a similar suranal plate in the Lepismids (fig. 2, "11"); although this plate in the Lepismids bears a terminal abdominal filament (fig. 2, *t*) not present in most Pterygotan insects, excepting the Ephemerids. The cercus-bearing podical plate of the lower Pterygotan insects (labeled "*p*" in figs. 8, 12, 6, etc.) which is apparently a portion of the eleventh segment, is also present in the Lepismids (fig. 2, "*p*."; the attachment of the cercus is indicated by the letter "*c*"). The tenth segment, designated by the numeral "10" in figs. 8, 12, and 4, is only slightly less pointed and projecting in the Pterygota there figured, than in the Lepismid depicted in fig. 2. The ninth segment is divided into a dorsal and a ventral portion 9*s* and 9*t* in the Pterygotan insect shown in fig. 8, and the same is true of the Lepismid (fig. 2); but in the Lepismid, a large stylus, or "megastylus" (fig. 2, "*m*"), is borne on the ventral plate of the ninth segment of the female, while in the majority of the lower Pterygota (with the exception of the Odonata) such a stylus is retained only on the tenth segment of the male. The dorsal valve of the ovipositor (fig. 5, "*d*") is borne on the ninth segment, and the ventral valve (fig. 5, "*v*") is borne on the eighth segment in the lower Pterygota, as in the case in the Lepismids[3] also (fig. 2, "*d*" and "*v*"). It is thus clearly evident that the terminal abdominal structures of the Lepismids are fundamentally and essentially similar to those of the lower Pterygotan insects, and the same is true of the head and other structures, so that Handlirsch's attempt to separate the Apterygota into a class or classes which do not include the Pterygota also, is quite unwarranted, and fails to take into consideration the fundamental resemblances which underlie all true relationships.

The terminal abdominal structures described above, remain but little modified in the lower Pterygotan insects, and it is rather surprising that they do not give more serviceable clews as to the relationships of the insects here discussed. They do however furnish some indications of relationships which are borne out by the study of other structures, and this would doubtless be even more evident if other more favorable material were available for comparison.

General usage requires that designations of a Latin or Greek derivation shall be applied in anatomical terminology, so that the

[3] This statement is based on figures of Lepismids by other investigators since I am not sure of the sex of the Lepismid here figured.

English designations "suranal plate" and "podical plate" are hardly suitable for universal application. In the following discussion the designation suranal plate has therefore been changed to the briefer term *pygidium,* and for the designation podical plate, the briefer term *subcercus* has been substituted, since the plate in question always bears the cercus, as the latter name implies.

The superorder Panplecoptera (composed of the Plecoptera, Dermaptera, Hemimerus and the Embiids) is typically an ovipositorless group, although certain earwigs, such as the one shown in fig. 9, have an ovipositor. In most members of this group, the eighth abdominal sternum does not overlap the following segment; but in certain Plectoptera there is a well-marked projection of the posterior margin of the eighth abdominal sternum extending backward over the succeeding sternum, and in many earwigs (fig. 9) the eighth abdominal sternum overlaps the following segment ventrally to a considerable extent. The tenth abdominal segment is relatively quite large in this superorder, and in most Dermaptera, Plecoptera and Embiids the pygidium ("11" of figs. 8 and 11) projects downward from the end of the tenth segment; although in the earwig shown in fig. 9, the pygidium (labeled "11" in the figure) projects backward and is curved in contour, somewhat like that of the Phasmid *Timema*[4] (Fig. 12, "11"). The cerci of some immature Plecoptera (fig. 4, *c*) have small ring-like segments similar to those of the cerci of Lepismids, while other Plecoptera (fig. 11) have cerci composed of cylindrical segments. In certain of the smaller Plecoptera, the number of segments in the cerci is reduced to only two, so that the difference in the cerci of the members of this superorder is not as great as would at first seem to be the case, and indeed, certain Dermaptera, such as *Diplatys* (or *Dyscritina*), in the immature stages have retained segmented cerci very like those of the Plecoptera.

The superorder Panorthoptera (composed of the Orthopteroid, Phasmoid, and Grylloblattoid insects) is typically an ovipositor-bearing one, and in this group, the ovipositor reaches its greatest development (in the lower Pterygotan insects), being usually composed of three valves (fig. 12, etc., *d, i,* and *v*), two of which are borne on the ninth segment, while the ventral one is borne on the

[4] An examination of subsequently received material would indicate that the curved contour is due to being crushed.

eighth segment. In the Phasmid *Timema,* the dorsal and ventral valves of the ovipositor (fig. 12, "*d*" and "*v*") have a more or less clearly demarked basal "segment" ("*b*" of fig. 12) and resemble those of the more primitive Blattids (fig. 5) in this respect. Traces of this basal portion of the valvæ occur in many other forms as well (figs. 7, 6, etc.), and in certain of the Orthoptera (fig. 10) a more or less vertical basal sclerite labeled "*f*" also occurs. In the Orthopteron shown in fig. 10, this sclerite articulates with a narrow "lora"-like sclerite labeled "*l*" which furnishes a firmer support for the movements of the ovipositor than the membranous region through which it extends, would give. In the more primitive Phasmids (fig. 12) the posterior region "*s*" of the eighth ventral segment does not project posteriorly to any great extent, as is true of many other representatives of this superorder. In certain Phasmids, however, this portion of the eighth ventral segment projects backward for a considerable distance and forms a sheath for the ovipositor, thus resembling quite closely the condition found in the Mantids (although this portion of the eighth segment is not shown in the Mantid depicted in fig. 7). The tenth abdominal segment is moderately well developed in this group, and the so-called suranal plate ("11" of figs. 6, 10, and 12) projects backward, instead of downward as in the preceding group. The region in question certainly appears more like merely a demarked portion of the tenth segment; but provisionally, at least, the generally accepted interpretation of it as the suranal plate (or suranale) has been adopted in the present paper. The cerci are usually one-segmented in this group, but in *Grylloblatta* (fig. 1), they are composed of cylindrical segments similar to those of certain Plecoptera (fig. 11). The pericercal organs occurring in rings about the segments of the cerci of the Grylloblattids (fig. 1, "*o*") are apparently sense organs, and their arrangement is quite different from the usual one, in this respect. The cerci of such Gryllids as *Œcanthus* (fig. 10, "*c*"), although but one-segmented, are longer than the ovipositor, and suggest a rather close relationship to *Grylloblatta* (fig. 1).

The superorder Pandictyoptera (composed of the Isopterous, Blattoid, and Mantoid insects) was possibly originally an ovipositor-bearing one, although many of the roaches have lost the ovipositor, and the Isoptera probably never developed one. Although it is not shown in the accompanying figures, the ventral portion of the ter-

minal abdominal segments (and frequently the dorsal portion also) is typically overlapped by a backward prolongation of the eighth segment. Holmgren, 1909 (p. 150), states that the *seventh* abdominal segment partially overlaps the following ones in the termites, and in his fig. 73 he designates this overlapping segment as the seventh. I think, however, that he has mistaken the actual *eighth* segment for the "seventh," due to the fact that the first abdominal segment is not devloped ventrally, in the termites. The tenth segment is moderately well developed tergally, but there is a tendency for the suranale to become rudimentary, especially in the Blattids. When the pygidium is developed (figs. 7 and 13) is usually projects downward, instead of backward as in the Panorthoptera. The cerci vary in form and in the number of segments composing them, but frequently the basal segments are more annular in outline in this group. The number of segments in the cerci may be reduced to one in this superorder also (fig. 5), thus showing that the tendency toward the reduction of the number of segments is quite widespread in all of the insects here discussed, making it practically impossible to make any general statements as to the number and character of the segments of the cerci in the different groups.

The Panplecoptera have apparently departed as little as any from the ancestral condition of the lower Pterygota, and it is rather remarkable that few if any of them seem to have retained any styli, since the Lepismids and other related Apterygotan insects are provided with numerous styli (fig. 2, "*st*" and "*m*"), and these structures occur in the males of the other two groups here discussed. The lack of an ovipositor in many representatives of the Panplecoptera is another feature which might appear to argue against the primitive character of this group, since a well-developed ovipositor occurs in many Lepismids, and other related Apterygota. The very primitive Apterygotan insects *Campodea* and *Anajapyx,* however, have no ovipositor, and the most primitive of all insects, the Protura, have no styli either, so that the absence of ovipositor and styli in the Plecoptera, etc., may be regarded as a retention of a primitive condition, rather than as a condition brought about by the loss of these structures. Furthermore, the development of the tenth abdominal segment ventrally, and the ring-like character of the ninth segment in the Plecoptera (figs. 4 and 11) seem to be primitive characters, since

a similar condition occurs in the lowest Apterygota (*Campodea, Eosentomon,* etc.). Although both types of cerci occur in the Panplecoptera, I am inclined to regard those with numerous small ring-like segments (fig. 4, "*c*") as the more primitive. The fact that the eighth abdominal sternum does not overlap the following ones is another primitive feature in the Plecoptera, and, on the whole, the Plecoptera seem to have departed as little as any living insects, from the original condition of the ancestors of the Pterygota. In many respects they are fully as primitive as the lowest fossil Pterygota, and a study of their structures is equally important from the standpoint of phylogeny. Furthermore, in dealing with living forms, there is the added advantage of being able to examine numerous details not preserved in fossil specimens, and to take into account the various biological data as well!

Before discussing the interrelationships of the three superorders here mentioned, their principal diagnostic characters may be briefly summarized in the following table. There are some exceptions to the general application of these characters, but, in the main, they hold good for the groups in question.

	Pandictyoptera (Usually)	Panorthoptera (Usually)	Panplecoptera (Usually)
Head	Opisthognathous (except Isoptera)	Hypognathous	Prognathous
Lateral cervicals	Corners touch in mid-ventral line	Do not touch	Do not touch
Ventral cervicals	Narrow transverse bands situated far forward	Usually none	Broader plates situated nearer prosternum
Posterior tergal wing process	Well developed	Usually not well developed	Absent or reduced
Meso-scutellum	Narrow, extending far forward	Not extending far forward	Not extending far forward
Meso-postscutellum	Reduced or wanting	Absent	Well developed (except earwigs)
Meso-coxae (from mesal surface)	Longer than broad	Short (except Gryllobla ttids)	Short
Tarsi	Pentamerous (reduced in some Isoptera)	Pentamerous to trimerous	Trimerous
Ovipositor	Developed in some (except Isoptera)	Well developed (except Gryllotalpids)	Absent (except earwigs)
Styli of male	Retained in some	Retained in some	Absent

Some of the representatives of each superorder have retained characters common to certain other superorders, and may therefore be spoken of as annectent between these groups. Thus, the Mantids and Isoptera resemble the Grylloblattids and Phasmids in some respects, while in others, they resemble the Embiids and Dermaptera. Similarly, the Grylloblattids and Phasmids resemble the Mantids and the Isoptera as well as the Embiids and Dermaptera: and, in the same way, the Embiids and Dermaptera resemble the Mantids and Isoptera as well as the Grylloblattids and Phasmids. Of these annectent forms, the most important are the Mantids, Grylloblattids and Embiids.

The older method of representing the relationships of the orders of insects by means of a dichotomously branching treee, drawn in one plane, is very unsatisfactory, since it does not allow for the fact that several lines of descent may approach one another from different directions (*i. e.,* the branches of the tree should be represented in *three* planes) and that one group of insects may be intermediate between two other groups, being hardly more closely related to one than to the other. If the relationships of the three superorders here discussed were to be representd graphically, it would be more exact to represent these superorders as forming the three apices of a triangle, each apex of which is connected with the other two by mutual bonds of relationship—or better yet, to represent them as three overlapping circles, each of which intersects the other two, and all having a certain amount of territory in common, although each circle forms a distinctly demarked group, when considered separately. In this area common to the three circles, the Embiids, Grylloblattids and Mantids would be placed, since these three members of the different superorders have a surprisingly large number of features in common, and are the most important "annectant" insects of the groups under discussion. Of slightly less phylogenetic importance are the Dermaptera, Phasmids and Isoptera, although they too furnish many valuable clues as to the relationships of the groups, so that if the interrelationships of the three superorders were expressed briefly in a formula, the annectent insects of less importance would be placed in parentheses as follows. "Mantids (Isoptera)—Grylloblattids (Phasmids) —Embiids (Dermaptera)."

In opposition to Dr. Walker's view as to the close relationship of

the Grylloblattids to the Blattids, I previously emphasized the remarkable structural resemblance between the Grylloblattids and Embiids in respect to their antennal segments, their cervical sclerites, the dorsal and pleural regions of their thoraces, etc. A study of the terminal abdominal segments and their appendages, however, would indicate that there is much to be said in favor of Walker's view, provided that instead of the Blattids, we consider the *Mantids* (which are very closely related to the Blattids). Thus, the terminal abdominal segments of the Grylloblattids (fig. 1) are very similar to those of the Mantids (fig. 7) in outline, and the same is true of their appendages, the ovipositor and cerci, while the Embiids have no ovipositor, and their cerci are composed of but two segments. In this connection, however, it should be remembered that even within the same order, some members of the group have no ovipositor while others have a well-developed one (*e. g.*, the Gryllids have a well-developed ovipositor, while the Gryllotalpids have none), and some Plecoptera have cerci composed of many segments, while other Plecoptera have cerci composed of but two segments. On the other hand, the cervical sclerites, and the thoracic sclerites remain remarkably constant or unmodified within an order and are therefore of greater importance from the standpoint of phylogeny! Furthermore, some members of the superorder Panplecoptera (notably the Dermaptera) have an ovipositor, and the segments of the cerci of other Panplecoptera are very similar in outline to those of the Grylloblattids, as may be seen by comparing fig. 11 with fig. 1; so that taking the Panplecoptera as a whole, the Grylloblattids are structurally slightly nearer to them than to the Pandictyptera, to which the Mantids belong. I would not minimize the remarkably strong resemblance between the Grylloblattids and Mantids, however, and would consider the Grylloblattids as structurally intermediate between the Mantids and Embiids; but their line of development parallels that of the Embiids somewhat more closely than it does that of the Mantids, so far as the least-varying structures are concerned.

Within the superorder Panorthoptera, the Grylloblattids are apparently nearer to the Gryllid-"Locustid" group, while the Phasmids are somewhat nearer to the "Acridids." In the superorder Panplecoptera, the Embiids are much closer to the Plecoptera, while the Dermaptera and Hemimerids are extremely closely related. In the

Pandictyoptera, the Mantids are somewhat closer to the Blattids than the Isoptera are, and the Isoptera are much nearer the Blattids than they are to the Mantids. The Psocids, which are placed near the Isoptera by Handlirsch (and are grouped with the Isoptera and Embiids by Enderlein) are in reality extremely closely related to the *Neuroptera* instead, and have departed but little from the ancestral condition of the Homoptera. The relationships here expressed are based upon a study of structures located in widely different parts of the body, and the agreement in a great number of details precludes the possibility of being deceived by a mere "convergence" or parallelism of development due to a similar mode of life, or other causes! It is necessary, however, first to take up each region of the body in a series of comparative studies of the most important structures, giving especial weight to those which vary but little within an order; and until this is done we have no really firm basis for determining the ancestry and interrelationships of the lower orders, for "one man's opinion is as good as another's" in such matters, and it is only by citing the facts of the case, and supporting one's statements by drawings of the parts in question, that one's opinions concerning the relationships of the orders of insects can carry any weight. On this account, it is preferable to defer the summing up of the numerous structural resemblances upon which the relationships here proposed are based, until the series of comparative anatomical studies (of which the present paper, and the one dealing with the lateral head, neck, and prothoracic regions, are a part) is more nearly completed, and the figures of the parts in question are available for reference in the discussion, since it would make too bulky and expensive a paper to attempt to publish all of these figures in a single article.

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ABBREVIATIONS.

b, basal sclerite of valve of ovipositor (Basivalvula).
s, cercus.
d, dorsal valvula of ovipositor (Survalvula).
f, basal sclerite of valvula of ovipositor (Valvifer).
i, intermediate valvula of ovipositor (Intervalvula) serving as egg-guide.
l, lora of ovipositor (Valvilora).
m, large stylus (Megastylus), usually only one retained in Pterygota.
o, pericercal (sense) organs.
p, podical plate (Subcercus), or cercus-bearing plate, a portion of the 11th segment.
s, subgenital plate (Subgenitale).
st, stylus.
t, terminal filament.
v, ventral valve of ovipositor (Subvalvula).

Numerals denote the number of the abdominal segment in question, the letter "*t*" written above the numeral denotes the tergum of that segment, and the letter "*s*" denotes the sternum. The numeral "11" denotes the suranal plate (Pygidium).

EXPLANATION OF PLATES XVI AND XVII.

(All figures are of females.)

Fig. 1. Terminal abdominal structures of *Grylloblatta;* lateral view of sinistral half of the body, showing 6th to the 11th segments.

Fig. 2. Terminal structures of a Lepismid; cerci removed and terminal filament partially cut off. Position of cercus indicated by letter "*c.*"

Fig. 3. Segments 6 to 10 of the Phasmid *Ectatosoma.*

Fig. 4. Terminal structures of an immature Plecopteron *Pteronarcys.*

Fig. 5. Terminal structures of a "Blattid," *Dasyposoma.* The overlapping portions of the preceding segments have been removed.

Fig. 6. Terminal structures of the Orthopteron *Paranabrus* (a "Locustid"). Ovipositor partially removed.

Fig. 7. Terminal structures of the "Mantid" *Stagmomantis* (?). Overlapping ventral portion of 8th segment removed, the point of attachment being indicated by black area.

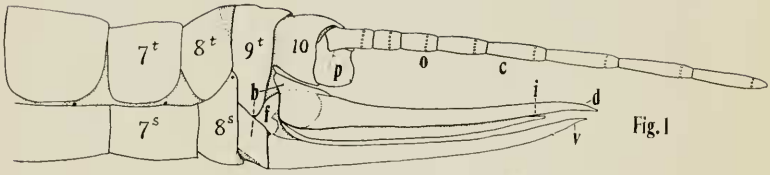


Fig. 1

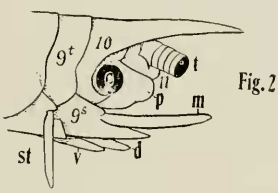


Fig. 2

Fig. 3

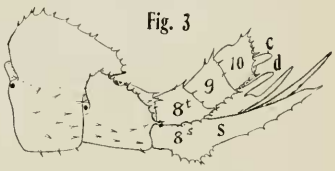


Fig. 4

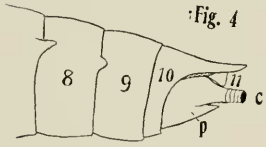


Fig. 5

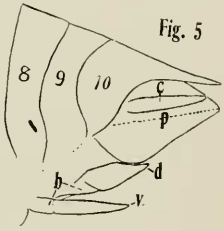


Fig. 6

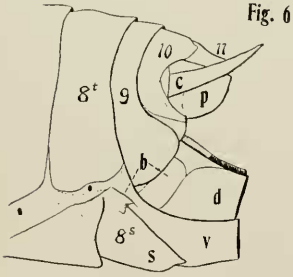
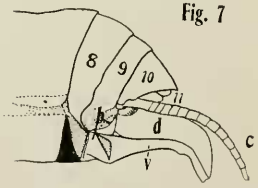


Fig. 7



Apterygota and Pterygota.